# THE FIBRO-VASCULAR SYSTEM OF THE APPLE (POME) AND ITS FUNCTIONS.

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(Plates xxi.-xxv.)

In the case of fleshy fruits, such as the Apple, there is a general impression that the entire edible substance consists of a succulent mass of tissue, without any of the stringy material which occurs in other parts of the tree; and even Sachs* states that the whole edible substance is composed of fundamental tissue, as distinct from the epidermis, on the one hand, and the vascular bundles, on the other. But when one remembers that the central core of the apple is surrounded by a relatively large mass of tissue, which grows and enlarges at a comparatively rapid rate, the necessity will be readily recognised for a framework of some kind for the soft parts; and there must be vessels or cells of some sort to convey the necessary food to the living and growing tissue. In other words, there must be a skeleton to prevent collapse, and conducting tissue to convey nourishment.

This is provided for in the fibro-vascular system, which looks very elaborate and complicated as a whole (Fig. 8), but when examined in detail, it is seen to consist of a definite number of strands, which give rise to numerous branches (Fig. 12.)

*General Structure of the Apple.*

The structure of the mature apple will now be dealt with, in so far as it is necessary for the understanding of the dis-

* Lectures on the Physiology of Plants, p.141.

tribution of the fibro-vascular bundles. It is attached to the end of the parent-branch by a longer or shorter stalk, and this is the channel through which nourishment is conveyed. If a longitudinal transverse section is made, it will show the essential parts (Figs. 2, 6).

The apple, unlike many other fruits, does not merely consist of seeds enclosed in a case, but surrounding that case there is the flesh of the apple. In the centre of the flower, there is a five-chambered ovary, and each chamber encloses normally two ovules. After fertilisation, the ovules become the "pips" or seeds, so that there are five carpels constituting the true fruit, with thick fleshy walls, but the inner face of each, bounding the seed-cavity, is smooth, firm, and cartilaginous in texture.

The five carpels enclosing the seeds constitute what is known as the "core" of the apple, but there is sometimes confusion over this, since the term is loosely applied to the five chambers containing the seeds, without including the fleshy walls of the carpels as well.

In each of the five carpels there is a wall of fleshy consistence, with an inner lining of horny texture. The outer boundary line is usually distinctly marked in a transverse section (Fig. 10), and each segment is more or less wedge-shaped, tapering to a point at the centre, where they all meet.

The boundary is obvious to the naked eye, because the cells composing it are different from those on each side. On the outside, the cells of the flesh are large and bladder-like; while, on the inside, the cells are rather smaller, and more elongated. The boundary itself consists of relatively small, tangentially elongated cells; and no doubt the difference in their size from those on either side, and the consequent crowding of their contents, render them distinct.

The flesh, covered by the skin, surrounds the core, and is added in order to enhance the attractiveness of the fruit, and increase the chances of the distribution of the seeds.

While the "core" is undoubtedly represented by the five carpels, there is a conflict of opinion as to the origin of the "flesh"; and, when narrowly looked into, it is seen that the structure of the apple is not so simple as it looks.

The flesh is generally considered to be the receptacle or top of the flower-stalk, enlarged and succulent, and investing the core. But there are some botanists who regard it as a thickened calyx-tube, or even as a composite structure, consisting of a calyx-tube, with the receptacle continued inside it as a sort of lining. All these views are without any direct evidence to support them, but the one most commonly held is that the flesh of the apple is the enlarged and succulent receptacle.

The depression at the apex is known as the "eye" of the apple, where the five leaves of the calyx still persist, and sometimes the remains of other parts of the flower as well.

*Transverse and Longitudinal Sections of the Apple.*

If a ripe apple is cut transversely about the middle, ten green spots are observed, arranged in a circle about midway between the centre and the skin (Fig. 1). These are the primary fibro-vascular bundles or strands of the apple; and if the section is allowed to dry, these points stand out distinctly. They are evidently developed in connection with the carpels, and there is one strand opposite each of the five chambers containing the seeds, and another in an intermediate position, making ten in all.

The "core" is separated from the "flesh" by a well-marked boundary line, which is attached to the top of the stalk below, and passes into the "eye" or calyx-end above, so that it is securely fixed (Fig. 5). Since the "core" is the seed-bearing body or true fruit, that explains why the fibro-vascular bundles are developed in connection with this most important organ. As affording strong corroborative evidence that the bundles are developed in connection with the carpels, when the abnormal number of six carpels occur (Fig.

2), there are twelve bundles instead of ten; and when there are four carpels, there are only eight strands (Fig. 3). In a longitudinal, median section of the apple each of these ten vascular bundles is seen to give rise to branches, which, in turn, branch again and so on, mostly towards the outside, although there are several branches on the inside (Fig. 7). From each of these ten strands, just as they are leaving the stalk, branches are given off to the outer and inner face of the seed-cavity, so that the seeds are well supplied. The main strands, however, are associated with the "flesh," and the diverging branches towards the outside do not divide much until they approach the skin, where they form a perfect network (Fig. 19). This vascular net envelops the flesh about one-quarter of an inch from the surface, and this wonderful and hitherto unsuspected structure not only unites the entire system of vessels, but it gives rise to the innumerable plume-like branches which reach even to the skin (Figs. 8 and 20). These arise from the boundaries of each mesh of the net, and they divide and subdivide in such a luxuriant manner that the ultimate branchlets interlace and intertwine, so as to form a seemingly continuous layer of conducting tissue beneath the skin. They penetrate the parenchyma cells immediately beneath the epidermis (Fig. 15), which are particularly rich in chlorophyll, and take an active part in the nutrition of the growing and swelling fruit. Brooks,* in his article on "The Fruit-spot of Apples," observes that they fade away into the surrounding tissue—"In the small veinlets, the vascular elements become fewer and fewer, finally giving place to long narrow cells that seem to be transitional between the vascular tissue and that of the apple-pulp." In a longitudinal section, the main strands are seen to come together again just at the "eye," where they pass out into the calyx, corolla, and stamens, so that the entire

* Bulletin of the Torrey Botanical Club. Vol. xxxv., p. 423, 1908.

flower, including the carpels, is fully supplied with vascular bundles.

*Vascular Bundles as a whole.*

It is not always practicable to get a complete and connected view of the vascular system of any particular organ, so as to understand how it is strengthened, and how it is nourished, how the delicate cells composing it are prevented from collapsing, and how the nutritive juices are conveyed to and from each part.

In the case of "skeleton" leaves, or leaves which have been bleached, the course of the vascular bundles may be easily followed. In net-veined leaves, such as those of the apple (Fig. 18), all the vascular bundles entering them are gathered into the midrib, and branches spread thence to all parts of the leaf. The branches or veins divide and subdivide until the meshes are exceedingly small, and the ultimate veinlets end free in the substance of the leaf. Every part of the leaf is traversed by this network of channels, and, at the same time, efficiently strengthened. But while flattened leaves may be readily bleached or even naturally skeletonised, I have never found a pulpy fruit, such as the apple, with the flesh decayed, and showing the complete framework naturally. I have succeeded, however, in separating out the bundles by artificial means. A healthy and mature Five-Crown apple was placed in a weak solution of potassium hydrate for a week, during which time the soft pulpy material was gradually removed, until, at the end of the week, the strands stood out quite distinct. It was next laid out in water, and, with brush and needle, the remaining soft parts were detached, so that ultimately there remained the ten strands with their ramifications, as photographed (Fig. 8). One would hardly imagine that a tender, juicy apple contained such a network of filaments, but without them the apple could never have grown to its full size, nor acquired its succulence and flavour. How this is so, will now be briefly indicated.

It is necessary to understand how the growing apple is nourished, before the wide distribution of the vascular system can be properly appreciated. It is not simply the developing seeds, with the case containing them, which require to be nourished as in ordinary fruits, but also the much larger mass of tissue outside of that, constituting the flesh. So much growth has to be made in a comparatively short time, that the apple-tree has to store up the necessary material during the previous season, for the early spring growth. The short branches known as fruit-spurs bear the fruit-buds, which are plump and well-nourished in order to give rise to the flowers. The material stored up in the branches is passed on to the flower when it is fertilised. It is easy to tell, within a few days, when fertilisation has occurred, for the flower-stalk stiffens and begins to swell. This stiffening and thickening are due to the rush of food-materials, and after the fall of the petals the stored-up food is practically exhausted. Then the young apple is partly nourished by the parent-plant, with its fresh green leaves, and partly by its own exertions. The water containing mineral matter in solution enters from the soil, passes along the roots, and up the stem, until it reaches the fruit-spurs. Here it enters through the stalk of the fruit, and is distributed along the various channels, until it bathes the tissues wherever the fine net-work reaches. The vessels are shown in one of the strands in Fig. 17.

The amount of water contained in a ripe and sound apple is 84 per cent. on an average, so that a proper water-supply is all-important for the formation of the fruit. The fruit increases in size, not so much from the multiplication as from the enlargement of the cells; and it can readily be understood how nicely the balance must be adjusted, in order to regulate the supply. The water-stream will be directed along the main channels towards the apex of the fruit, and if the cells are overgorged, then rupture of the tissue may result; and if there is a dearth of water, a concentration of the contents of the cells may follow.

The leaves of the tree are now busy manufacturing starch, some of which will be transported in the soluble form of sugar to nourish the growing fruit, which is, however, able, to a certain extent, to provide for its own needs in this respect. The chlorophyll-containing cells of the hypodermal layer are also producing starch under the influence of sunlight, so that from these two sources—the green leaves, and the green layer of the fruit—abundance of starch is formed in a normal season. This has to be rapidly transported, when the fruit is swelling, from the place of manufacture to the tissues where wanted. The insoluble starch is rendered soluble by means of a ferment, and the use of the innumerable connected and branching veinlets in the hypodermal tissue will now be evident. In the fruit-growing season, there is a great drain upon the plant's resources ; and the manufactured starch must be quickly removed, in order to make room for fresh supplies. "The solution of starch is hastened by the continual removal of the sugar produced."*

But the green apple is not merely a consumer, using the material supplied, for building up its tissues ; it requires to store up material towards the period of ripening, and starch grains are invariably found in the cells of unripe fruit. "The percentage of starch in apples varies entirely with the age of the fruit ; in green apples it may amount to five per cent. or more, while in the completely ripened fruit it is altogether wanting."†

The vascular bundles, as a whole, can now be understood. In a transverse section of the stalk just as it enters the fruit (Fig. 11), there are ten vascular bundles, although sometimes two adjoining may become confluent. These, on entering the fruit, spread out out to form ten main trunks with numerous branches, and conveniently situated about midway between the skin and the centre.

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* Pfeffer, The Physiology of Plants. Vol. i., p. 505.

† Browne, "A Chemical Study of the Apple and its Products." Pennsylvania Department of Agriculture. Bulletin 58.

The earliest branching and the most direct course is towards the carpels and the seeds, then the flesh is supplied by numerous diverging branches which unite to form a network of vessels, and finally terminate, beneath the skin, in a perfect maze of the most delicate forked veinlets. So richly is the apple supplied with a connected system of vascular bundles, that it would be difficult to find an area of any size without them.

The reason for this is evident, since the developing fruit must be richly supplied with food-materials to maintain the rapid growth. The water, containing mineral matter in solution, the so-called "crude sap," is conveyed by the wood-portion of each bundle with its vessels and tracheids. The solution of organic food-material, the so-called "elaborated sap," passes along the bast-portion with its sieve-tubes and associated cells; and by means of numerous cross-connections between the two kinds of tissues, there is a blending of the "crude" and "elaborated" saps, which results in the formation of proteid substance; and this, in contact with the living protoplasm, becomes converted into the living substance itself.

The vascular system must not be conceived of as a vast network of tubes conveying food-material to a definite terminus, but as being tapped on the way by living tissues wherever growth is going on, or storage is required. The movement of the food-materials takes place in whatever direction supplies are wanted, and, even in the same cell or vessel, there may be a flow in opposite directions at the same time.

*The Skeleton.*

The apple starts as a very small fruit, but gradually grows to a good size, and therefore requires a framework to support the fleshy portion. There is great variation in the size and weight of apples. Rome Beauties have reached 19 ozs., and Rymers 22 ozs., in a Victorian orchard during the past season; but the heaviest known to me grew on a six-year old tree in the same orchard. It was a Munroe's Favourite, green when picked, and weighing 2 lbs. 2 ozs. Such a mass of pulpy tissue would collapse by its own weight, unless there were some means of strengthening it. The distended cell-walls of the tissue itself would tend to stiffen the whole, just as in a firm leaf when the cells are all turgid, but strengthening rods are required as well. There are ten of these curved supports, normally equidistant from each other, diverging from the stalk at the base, and becoming united again at the top, just beneath the eye. These strengthen the whole structure, like so many curved ribs, and the various branches form lesser supports. It will be observed that this system of strengthening is not merely mechanical; it is also a living mechanism, which has to grow and expand according to the strain it has to bear.

The growth of the core and of the flesh concurrently, requires a nice adjustment of the various contributing factors. The enlarging core is richly supplied with a fine network of vessels for its own immediate use, and there are also branches stretching from it at various angles, traversing the flesh, and firmly rooted beneath the skin. As the flesh enlarges, these branches stretch in unison with it, and they are so tightly stretched that they resemble so many stays keeping the core in position. This is shown in Fig.9, where some of the strands are dissected out, and while serving as holdfasts, they also convey nourishment when required.

The skin is likewise a form of skeleton, giving firmness and consistency to the entire fruit, although its main function is to regulate transpiration. The thick-walled mother-cells of the epidermis are divided by thinner walls into more or less quadrilateral daughter-cells, and the appearance presented by them has given rise to the name of "window-cells"(Figs.13, 14). The rapid expansion of the surface is provided for, to keep pace with the internal growth, by means of these window-shaped cells; for although in uninterrupted contact with each other, when they stretch, a new window is inserted between, and thus the superficial area is increased.

*Vascular bundles in relation to the Seeds.*

That the vascular bundles are developed primarily in connection with the "core" comprising the carpels, and gradually spread out into the fleshy receptacle is evident from various considerations. When a coloured fluid is injected into the stalk of the apple, it first spreads out into the cavity containing the seeds and thus the "pips" or seeds are the first to be supplied with the nutritive fluid. But very striking evidence is also afforded that the development of the seed influences the growth of the fleshy receptacle, for when only some of the ovules are fertilised and produce seeds, it is found that the apple is rather one-sided. The seedless portion does not grow so rapidly as the other, because the vessels conducting the food-materials are not so luxuriantly developed. Thus the position of the bundles in the wall of the the core, their direct communication with the seeds, and their sparing development when no seeds are formed, all point to an essential relationship between the two.

But there may be overgrowth or irregular growth as well as undergrowth in the apple, according to the nature of the season. Under certain conditions of heat or moisture, the supplies coming from the roots and the leaves, together with those manufactured by the apple itself, will produce abnormal growth, especially when transpiration is not active, and the water accumulates in the cells. A well-balanced ration is just as necessary for the healthy plant as for the healthy animal, and whatever disturbs the equilibrium will tend to produce a disordered nutrition. Even the keeping quality of fruit is affected when the specimens are overgrown. Beach and Clark* in their Bulletin on "New York Apples in Storage," remark that—"It is a matter of common observation that specimens that are very large for the variety do not keep as well as those of medium size and firmer texture. This is remarked by several cold-storage men. Such fruit may be produced on young trees, or on mature trees making excessive growth, or carrying a light crop.'

*Vascular bundles in relation to each other.*

The primary vascular bundles in the apple, just as in other portions of the tree, do not remain isolated and disconnected, but, by the anastomoses which take place, particularly towards the periphery, there is continuity throughout. The entire system

* New York Agricultural Experiment Station. Bulletin 248, 1904.

is comparable, in this respect, to the anastomosing veins and arteries of the human body, only we must be on our guard against speaking of "circulatory" tissues, or of the "circulation" of water and foods, as if there were a central organ from and to which the nutritive fluids were directed. On the other hand, we must remember that, even in the apple, there is a connected, and not a scattered system of vascular bundles (as Strasburger erroneously states), which branch out from the stalk, and distribute food-materials to every part, passing along the inner wall of each of the five chambers to supply nourishment to the seed, and then spreading out among the cells of the flesh.

The fruit is a kind of central depôt, to which all the various ingredients, which go to make up a perfect food, are conveyed. The water containing mineral matter in solution from the root, and the starch conveyed in the soluble form of sugar from the leaves, meet and unite to form the organic food-supplies, the so-called elaborated sap, which passes through the stalk into the fruit, and there, in contact with the living protoplasm, builds up new tissue.

The fruit itself supplies an extra amount of starch, to be stored up, and utilised when ripening occurs. As the fruit ripens, this stored-up starch is gradually converted into sugar, and instead of being sour and disagreeable, it acquires the pleasant taste and delicious flavour of the world-renowned fruit of temperate climes. The sweetness of an apple, however, does not depend altogether upon an excess of sugar, as is generally supposed, but rather upon an absence of malic acid, for sour apples are frequently found to contain more sugar than fruit of a sweeter kind.* The taste of an apple, therefore, will depend mainly on the diminished acidity, but also partly on the percentage of sugar present.

Thus as the result of supplies drawn from the soil and the air, and distributed by means of a highly elaborate and effective vascular system, there is produced the shapely, coloured, nutritive, and finely flavoured apple, which contains the seed, the supreme effort of the tree's existence.

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* Browne, "A Chemical Study of the Apple and its Products," p 14.

## EXPLANATION OF PLATES XXI.-XXV.

Plate xxi.

Fig. 1.—Transverse, median section of an apple, showing the ten primary fibro-vascular bundles in the form of ten greenish dots, arranged in a circle, each bundle being either opposite to, or intermediate with each of the five carpels.

Fig. 2.—Thin, transverse slice of Rome Beauty, showing twelve fibro-vascular bundles, corresponding to the six carpels. The bundles are seen branching outwardly, and becoming much subdivided just beneath the skin.

Fig. 3.—Transverse, median section of Rome Beauty, showing eight fibro-vascular bundles, when there are only four carpels.

Fig. 4.—Diagrammatic, transverse section showing how the branches of each bundle ultimately divide in a forked manner, and break up into minute branchlets, intertwining with each other just beneath the skin.

Plate xxii.

Fig. 5.—Longitudinal, median section of an apple, showing the wall of the "core" attached below to the top of the stalk, and above passing into the "eye."

Fig. 6.—Thin, longitudinal slice of an apple, showing vascular bundles running lengthwise from the stalk, along the outer wall of the "core," and the forked branches beneath the skin.

Fig. 7.—Diagrammatic, longitudinal section, showing one of the primary vascular bundles diverging from the top of the stalk, and giving rise to secondary branches supplying the "core," on the one hand, and the "flesh," on the other. The branches to the core envelop the carpels in a fine network, so that every part is reached by the conducting tissue. The various branches supplying the flesh from each of the primary bundles also form a united network extending from the "eye" to the stalk, and completely surrounding the bulk of the flesh. On the outside, the strands of this network give off plume-like branches reaching to the skin, and breaking up into innumerable, fine filaments which intertwine.

Fig. 8.—Fibro-vascular system as a whole, showing the main trunks and the numerous branches. The network of vessels is seen covering the carpels in the interior and the outer branches end in a perfect maze of branchlets beneath the skin.

Plate xxiii.

Fig. 9.—Longitudinal, median section, with the flesh surrounding the core removed. The top of the stalk is shown still attached to the core, which extends to the "eye" at the apex. From the top of the stalk, a primary vascular bundle, on each side, surrounds the core

branching inwardly and covering the seed-cavity with a fine network of vessels, and branching outwardly towards the surface.

Fig. 10.—Transverse, median section of core, showing the flower-like arrangement of the carpellary walls, and the ten primary vascular bundles associated with them.

Fig. 11.—Transverse section of stalk just as it enters the fruit, showing the ten fibro-vascular bundles. At this level, there were four bundles single, and the remaining six formed three pairs. At the base of the core, they broke up into ten distinct vascular bundles, as shown in the next figure ($\times 30$).

Fig. 12.—Transverse section of stalk, where the vascular bundles diverge, showing ten strands radiating from it.

Plate xxiv.

Fig. 13.—Surface-view of epidermis, showing the thick-walled mother-cells divided into the thinner-walled daughter-cells, known as "window-cells," from their appearance ($\times 100$).

Fig. 14.—Surface-view of epidermis, with the contents of the daughter-cells retained ($\times 100$).

Fig. 15.—Cross-section through the skin of an apple, showing the epidermis and hypodermal layer into which the ultimate branchlets of the vascular bundles penetrate. There is the cuticle of the epidermis, about $12\mu$ in thickness, standing out clearly, and surmounted by a thin deposit of wax; the brick-shaped epidermal cells, and usually four or more layers of cells in the hypoderm tangentially elongated ($\times 100$).

Fig. 16.—Transverse section of a fibro-vascular bundle, showing the xylem, with numerous vessels below, and the phloem with sieve-tubes above. The parenchymatous cells of the flesh adjoining the vascular bundle are usually narrower, and smaller than the ordinary cells ($\times 100$).

Fig. 17.—Longitudinal section of vascular bundle, showing the spiral vessels of the xylem ($\times 100$).

Fig. 18.—Leaf of apple showing midrib, with diverging veins and veinlets forming a network. The number of vascular bundles entering the petiole is three.

Plate xxv.

Fig. 19.—Oblique view of apple, with the outer flesh removed, showing the enveloping network of vascular bundles, with the projecting, plume-like branches arising from the strands of each mesh.

Fig. 20.—Plume-like branches, slightly enlarged.

Fig. 21.—General view of network and plume-like branches, with some of the flesh still adhering to the "eye"-end.